

## Comparative wood and leaf anatomy of the *Cecropiaceæ* (Urticales)

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**Summary** : The wood and leaf anatomy of the 6 genera of the *Cecropiaceæ* are described in detail. The anatomical data are compared with those of the allied *Moraceæ* and *Urticaceæ*. The relationship between habit, habitat, and anatomical characters is discussed, as well as the relationships within the family. Based on anatomical data the genus *Poikilospermum* should be included in the family *Urticaceæ*.

**Résumé** : Une analyse anatomique détaillée du bois secondaire et de la feuille des 6 genres constituant la famille des *Cecropiaceæ* est présentée. Les résultats ont été comparés à ceux obtenus pour des familles proches : *Moraceæ* et *Urticaceæ*. Les rapports entre les biotopes, les formes biologiques des plantes et les caractères anatomiques ont été considérés, ainsi que les affinités au sein de la famille. Les résultats anatomiques indiquent que le genre *Poikilospermum* doit être placé dans la famille des *Urticaceæ*.

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### INTRODUCTION

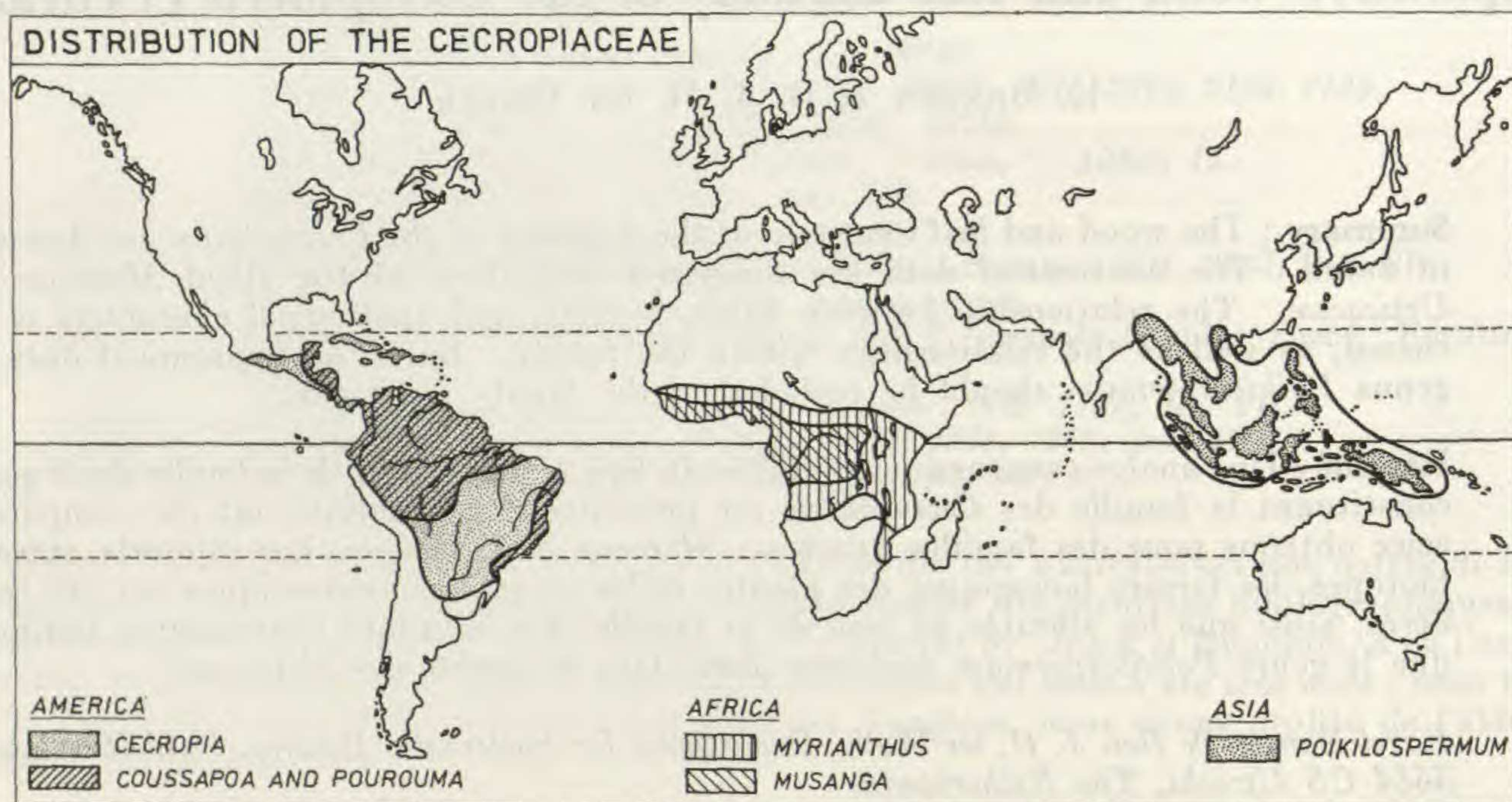
Recent taxonomic studies of the *Moraceæ*, especially those from tropical America and Africa, have been carried out by C. C. BERG, Institute for Systematic Botany (Utrecht), while anatomical studies of this family were conducted by S. M. C. TOPPER (wood) and A. KLOOS (leaf) also at Utrecht. In 1978, BERG separated the *Cecropiaceæ* from the *Moraceæ*. A detailed anatomical study of this new family to complete the leaf and wood anatomical survey, therefore seemed desirable.

The *Cecropiaceæ* constitute a pantropical family of about 200 species in 6 genera. Among the genera we find hemi-epiphytic scramblers, shrubs or trees with aerial roots, sometimes lianas, and small to tall trees, often with stilt-roots. Most species of *Coussapoa* and *Poikilospermum* are hemi-epiphytes, while the species of *Cecropia* and *Musanga* are commonly pioneer plants, and most species of *Pourouma* and *Myrianthus* are small or medium-sized trees of the lower stories of more or less open and disturbed forests.

In ENGLER's system of the *Moraceæ* (1889) the neotropical genera *Cecropia*, *Coussapoa*, and *Pourouma*, together with the African genera *Musanga* and *Myrianthus*, and the Asiatic genus *Poikilospermum* (= *Conocephalus*), constituted the subfamily *Conocephaloideæ*. CHEW WEE-LEK (1963) suggested to transfer the small-seeded genera *Cecropia*, *Coussapoa*, *Musanga*, and *Poikilospermum* to the *Urticaceæ*, but retained the big-seeded genera *Myrianthus* and *Pourouma* in the *Moraceæ*. CORNER (1962) transferred the whole subfamily

*Conocephaloideæ* to the *Urticaceæ* mainly on the basis of similarities in the characters of the ovary : a single stigma and a basally attached orthotropous ovule.

The genus *Poikilospermum* has been monographed by CHEW WEE-LEK (1963), the genera *Musanga* and *Myrianthus* by DE RUITER (1976).



Anatomical studies of the subfamily *Conocephaloideæ* (= *Cecropiaceæ*) were made by RENNER (1907), and of *Cecropia* by RICHTER (1898). RENNER noticed the isolated position of the genus *Conocephalus* (= *Poikilospermum*) based on the structure of the stomata and glands, and the presence of cystoliths. He pointed out the remarkable anatomical similarity between the American and African genera and showed that these genera fall into two groups on the basis of their adaxial glands ; viz. *Musanga*, *Myrianthus* and *Pourouma* on the one hand and *Cecropia* and *Coussapoa* on the other. More anatomical data have been given by SOLEREDER (1899, 1908), and METCALFE & CHALK (1950).

Finally, BERG (1978) created the *Cecropiaceæ* also using anatomical data as far as known to him from literature.

#### MATERIALS AND METHODS

The majority of the wood samples for this study was taken from the Utrecht wood collection, while the leaves were taken from vouchers deposited in the herbarium in Utrecht. Herbarium vouchers of all specimens, identified by C. C. BERG and E. G. B. KIEFT (*Pourouma*) are located in Utrecht. Information on collector's numbers and wood collection accession numbers (abbreviations according to STERN, 1978), locality and diameter of the samples, is given in the tables 1 and 2. This study is based on 84 wood specimens representing 6 genera and 45 species, apart from 45 leaf specimens representing 6 genera and 34 species. Sections and macerations were prepared according to standard techniques, and embedded in Canada balsam and in glycerin respectively. The wood anatomical terminology used is that proposed by the Committee on Nomenclature of the I.A.W.A. (1964).

TABLE 1 : Leaf specimens of the *Cecropiaceæ* studied.

| SPECIES                                 | LEAF       |           | COLLECTOR                    | COLLECTION LOCALITY   |
|---|------------|-----------|------------------------------|-----------------------|
|   | COLLECTION | HERBARIUM |                              |                       |
| <i>Cecropia latiloba</i> Miq.           | B-404      | 332521 B  | Prance & Berg P 17586        | Brasil, Amazonas      |
| <i>C. obtusa</i> Trec.                  | B-405      | 378826 B  | Prévost 732                  | Fr. Guiana            |
| <i>C. sciadophylla</i> Mart.            | B-406      | 258202 B  | Roberts L.B.B. 12791         | Surinam               |
| <i>C. surinamensis</i> Miq.             | B-407      | 253593 B  | L.B.B. 12739                 | Surinam               |
| <i>C. sp.</i>                           | B-459      |           | Hortus Baarn 2/7, cult.      | Netherlands (Cult.)   |
| <i>Coussapoa angustifolia</i> Aubl.     | B-420      | 211911 B  | van Donselaar 2569           | Surinam               |
| <i>C. asperifolia</i> Trec.             | B-436      | 362253 B  | Oldeman B 2538               | Fr. Guiana            |
| <i>C. latifolia</i> Aubl.               | B-416      | 81393 B   | Mennega 271                  | Surinam               |
| »                                       | B-417      | 332696 B  | Prance & al. 58783           | Brasil, Para          |
| »                                       | B-437      | 332533 B  | Lieras & Monteiro P 19661    | Brasil                |
| »                                       | B-438      | 384674 B  | Heyde & Lindeman 78          | Surinam               |
| <i>C. microcarpa</i> (Schott) Rizzini   | B-421      | 270318 B  | Lindeman & al. 5682          | Brasil, Parana        |
| <i>C. microcephala</i> Trec.            | B-439      | 390327 B  | Maas 2478                    | Guyana                |
| <i>C. nitida</i> Miq.                   | B-422      | 332608 B  | Berg & al. P 17592           | Brasil, Amazonas      |
| »                                       | B-440      | 393714 B  | Huashikat 1585               | Peru                  |
| <i>C. orthoneura</i> Standl.            | B-418      | 362170 B  | Revilla 1847                 | Peru                  |
| »                                       | B-419      | 277078 B  | Prance & al. 14029           | Brasil, Amazonas      |
| »                                       | B-441      | 393716 B  | Liesner 8750                 | Venezuela             |
| <i>C. ovalifolia</i> Trec.              | B-442      | 393720 B  | Diaz & Osoreo 618            | Peru                  |
| <i>C. panamensis</i> Pitt.              | B-443      | 370065 B  | Neill L984                   | Nicaragua             |
| <i>C. parvicops</i> Standl.             | B-444      | 370061 B  | Hammel 2176                  | Panama                |
| <i>C. trinervia</i> Mildbr.             | B-445      | 393718 B  | Rosa & Vilar 2874            | Brasil                |
| <i>C. villosa</i> P. & E.               | B-446      | 393717 B  | Pires & Santos s.n.          | Brasil                |
| <i>Musanga cecropioides</i> R. Br.      | B-408      | 257909 B  | Versteegh & al. 52           | Ivory coast           |
| »                                       | B-450      | 159447 B  | Mann s.n.                    | W. trop. Africa       |
| <i>Myrianthus arboreus</i> Pal. Beauv.  | B-411      | 41498 B   | Deistel 428                  | Cameroon              |
| <i>M. libericus</i> Rendle              | B-409      | 257646 B  | Versteegh & al. 24           | Ivory Coast           |
| <i>M. serratus</i> (Trec.) B. & H.      | B-410      | 202186 B  | Mann 2273                    | W. trop. Africa       |
| <i>Poikilospermum abnorme</i> Chew      | B-415      | 11223 B   | Eyma 3536                    | Indonesia, Celebes    |
| <i>P. amboinense</i> Zipp. ex Miq.      | B-412      | 34062 A   | Docters van Leeuwen          | Indonesia, NW. Guinea |
| »                                       | B-413      | 34111 A   | Docters van Leeuwen          | Indonesia, NW. Guinea |
| <i>P. inæquale</i> Chew                 | B-403      |           | Jacobs 9575                  | Papua, NW. Guinea     |
| <i>P. subtrinervium</i> (Miq.) Chew     | B-414      | 33780 A   | Mandi 25                     | Indonesia, Borneo     |
| <i>Pourouma acuminata</i> Mart. ex Miq. | B-580      |           | Jobert 682                   | Brasil, Potomayo      |
| <i>P. albistipulata</i>                 | B-396      |           | Steyermark & al. 103026      | Venezuela             |
| <i>P. cecropiifolia</i> Mart.           | B-579      |           | Krukoff 5327                 | Brasil, Acre          |
| <i>P. cuspidata</i> Warb.               | B-397      | 38698 A   | Krukoff 8373                 | Brasil, Amazonas      |
| <i>P. feruginea</i> Standl.             | B-398      |           | Coelho & al. 339             | Brasil, Amazonas      |
| <i>P. guianensis</i> Aubl.              | B-399      | 355615 B  | Berg & al. BG 772            | Brasil, Para          |
| <i>P. lævis</i> Benth.                  | B-400      | 673930 B  | Boschwezen 4010              | Surinam               |
| <i>P. minor</i> R. Ben.                 | B-014      | 358752 B  | Schunke 8487                 | Peru, Amazonas        |
| <i>P. mollis</i> Trec.                  | B-581      |           | van Donselaar 1681           | Surinam               |
| <i>P. velutina</i> Miq.                 | B-447      | 361783 B  | Prance 21011                 | Brasil, Amazonas      |
| <i>P. sp.</i>                           | B-448      |           | Berg & Nee 355               | Panama, Canal Zone    |
| <i>P. sp.</i>                           | B-449      |           | Herbario Adolfo Tonduz 12930 |                       |

TABLE 2 : Wood specimens of the *Cecropiaceæ* studied.

| SPECIES                             | XYLARIUM | COLLECTOR                                    | COLLECTION LOCALITY | MINIMUM DIAMETER (cm) |
|-------------------------------------|----------|--|---------------------|-----------------------|
| <i>Cecropia burriada</i> Cuatr.     | U 25025  | <i>Cuatrecasas 15260</i>                     | Colombia, Choco     | 10                    |
| <i>C. concolor</i> Willd.           | U 20959  | <i>Prance &amp; Berg P 19817</i>             | Brasil, Amazonas    | 9                     |
| <i>C. ficifolia</i> Snethl.         | U 20919  | <i>Prance &amp; Berg P 18526</i>             | Brasil, Amazonas    | 9                     |
| <i>C. garcia</i> Standl.            | U 27511  | <i>Cuatrecasas 16467</i>                     | Colombia, Choco     | 10                    |
| <i>C. monostachya</i> C. Berg       | U 23612  | <i>Berg, Maas &amp; ter Welle 416</i>        | Equador             | 2                     |
| <i>C. obtusa</i> Trec.              | U 21569  | <i>Smith 2164</i>                            | Guyana              | 10                    |
| <i>C. peltata</i> L.                | U 25719  | <i>Süss 17</i>                               | Cuba                |                       |
| <i>C. riparia</i> Warb.             | U 21655  | <i>Smith 3426</i>                            | Guyana              |                       |
| <i>C. sciadophylla</i> Mart.        | U 179    | <i>Stahel 179</i>                            | Surinam             | 10                    |
| »                                   | U 2146   | <i>B.B.S. V16</i>                            | Surinam             | 9                     |
| »                                   | U 2296   | <i>Ellenberg</i>                             | Peru                | 10                    |
| »                                   | U 2379   | <i>Lindeman 3617</i>                         | Surinam             | 6                     |
| »                                   | U 5124   | <i>BAFOG 39M</i>                             | Fr. Guiana          | 6                     |
| »                                   | U 7581   | <i>Krukoff 6237</i>                          | Brasil, Amazonas    | 2                     |
| »                                   | U 17503  | <i>Maguire &amp; al. 55577</i>               | Surinam             | 15                    |
| »                                   | U 19622  | <i>Krukoff 4789</i>                          | Brasil, Amazonas    | 7                     |
| »                                   | U 19929  | <i>Krukoff 5389</i>                          | Brasil, Acre        | 2                     |
| »                                   | U 23290  | <i>Heyde 710</i>                             | Surinam             | 7                     |
| <i>C. telealba</i> Cuatr.           | U 27512  | <i>Cuatrecasas 18353</i>                     | Colombia, Choco     | 14                    |
| <i>Coussapoa angustifolia</i> Aubl. | U 4470   | <i>Lindeman 6545</i>                         | Surinam             | 9                     |
| <i>C. asperifolia</i> Trec.         | U 3917   | <i>Lindeman 5709</i>                         | Surinam             | 25                    |
| »                                   | Dw 5596  |  | Brasil              | 10                    |
| <i>C. batavorum</i> Akk. & Berg     | U 25671  | <i>v. Rooden, ter Welle &amp; Topper 700</i> | Colombia, Choco     |                       |
| <i>C. contorta</i> Cuatr.           | U 25192  | <i>Cuatrecasas 14284</i>                     | Colombia, Choco     | 6                     |
| <i>C. hololeuca</i> Miq.            | U 27072  | <i>Berg &amp; Akkermans 1142</i>             | Equador             |                       |
| <i>C. latifolia</i> Aubl.           | U 22728  | <i>Lindeman &amp; Heyde 78</i>               | Surinam             | 15                    |
| <i>C. trinervia</i> Spruce          | U 27032  | <i>Berg &amp; Akkermans 1038</i>             | Equador             | 6                     |
| <i>C. villosa</i> P. & E.           | U 20911  | <i>Prance &amp; Berg P. 18455</i>            | Brasil, Amazonas    | 8                     |

TABLE 2 (Contd.).

| SPECIES  | XYLARIUM     | COLLECTOR               | COLLECTION LOCALITY    | MINIMUM DIAMETER (cm) |
|--|--------------|-------------------------|------------------------|-----------------------|
| <i>Musanga cecropioides</i> R. Br.             | U 6445       | ex RBHw                 | Cameroon               | 18                    |
| »  | U 24230      | Louis 13501             | Congo                  | 30                    |
| »  | U 24231      | Donis 435               | Congo                  | 30                    |
| »  | U 24386      | Antoine 283             | Congo                  | 50                    |
| »  | U 24489      |                         | Angola                 |                       |
| »  | U 24613      | ex MAD-SJRw 15253       | Liberia                | 20                    |
| »  | U 24614      | ex MAD-SJRw 15799       | Liberia                | 20                    |
| »  | U 24622      | ex MADw 36807           | Ivory Coast            | 20                    |
| »  | Dw 5609      | Antoine s.n.            | Zaire                  | 20                    |
| <i>M. leo-ereræ</i> Haum.                      | U 24232      | Bauxin 1021             | Rwanda                 | 75                    |
| <i>Myrianthus arboreus</i> Pal. Beauv.         | U 20313      | de Briey 49             | Zaire                  |                       |
| »  | U 24385      | R 478-80                | Tanganyika             | 15                    |
| »  | U 24446      | Leeuwenberg 9656        | Cameroon               | 7                     |
| »  | U 24619      | ex MADw 36828           | Ivory Coast            | 10                    |
| »  | U 24632      | ex MADw 32716           | Congo                  |                       |
| <i>M. holstii</i> Engl.                        | U 15509      | ex RBHw 1542            | East Africa            | 8                     |
| »  | U 15525      | ex RBHw 1577            | East Africa            | 8                     |
| »  | U 24234      | Bouxin 1291             | Rwanda                 |                       |
| <i>M. libericus</i> Rendle                     | U 24235      | Cooper 285              | Liberia                |                       |
| »  | U 24615      | ex MAD-SJRw 13778       | Liberia                |                       |
| »  | U 24617      | ex MAD-SJRw 15198       | Liberia                |                       |
| »  | U 24621      | ex MADw 36781           | Ivory Coast            | 15                    |
| <i>M. serratus</i> (Trec.) B. & H.             | U 24618      | ex MAD-SJRw 15110       | Liberia                | 4                     |
| <i>Poikilospermum amboinense</i> Zipp. ex Miq. | U 26781      | Lam 647                 | Indonesia, NW Guinea   | 1,5                   |
| <i>P. inæquale</i> Chew                        | U 26780      | Docters v. Leeuwen 9671 | Indonesia, NW Guinea   | 1                     |
| <i>P. naucleiflorum</i> Euse                   | U 27519 RTIw | 1507/i22-H 1868-274     |                        | 3                     |
| <i>P. suaveolens</i> (Bl.) Merr.               | U 27070      | Jacobs 8502             | Indonesia, Sumatra     | 3,5                   |
| »  | Pw/U 27516   | de Vogel 4516           | Indonesia, N. Moluccas | 2                     |
| <i>P. sp.</i>                                  | Lw/U 27517   | Jacobs 9575             | Papua NW Guinea        | 2                     |
| <i>P. sp.</i>                                  | U 27518 RTIw | Koorders 35779 B        | Indonesia, Java        | 1,5                   |

TABLE 2 (Contd.)

| SPECIES                                  | XYLARIUM | COLLECTOR                                   | COLLECTION LOCALITY | MINIMUM DIAMETER (cm) |
|--|----------|---|---------------------|-----------------------|
| <i>Pourouma acuminata</i> Mart. ex Miq.  | U 16196  | <i>Krukoff 8427</i>                         | Brasil, Amazonas    | 10                    |
| <i>P. acutiflora</i> Trec.               | U 13744  | <i>Hatschbach &amp; Lindeman 13537</i>      | Brasil, Parana      | 15                    |
| <i>P. apiculata</i> Spruce               | Dw 5640  |   | Brasil              | 10                    |
| <i>P. aspera</i> Trec.                   | U 25405  | <i>Cuatrecasas 15071</i>                    | Colombia            | 8                     |
| <i>P. cecropiifolia</i> Mart.            | U 19763  | <i>Krukoff 5109</i>                         | Brasil, Amazonas    | 18                    |
| »  | U 19903  | <i>Krukoff 5327</i>                         | Brasil, Acre        | 4                     |
| <i>P. chocoana</i> Standl.               | U 24925  | <i>Cuatrecasas</i>                          | Colombia, Choco     | 5                     |
| <i>P. digitata</i> Trec.                 | Dw 2225  | <i>M 2214</i>                               |                     | 10                    |
| »  | U 17970  | <i>Oldenburger, Norde &amp; Schulz 1406</i> | Surinam             | 11                    |
| <i>P. guianensis</i> Aubl.               | U 11140  | <i>Florschütz &amp; Maas 3132</i>           | Surinam             | 4                     |
| »  | U 19274  | <i>Krukoff 1297</i>                         | Brasil, Amazonas    |                       |
| »  | U 20956  | <i>Prance &amp; Berg P 18250</i>            | Brasil, Amazonas    | 20                    |
| »  | U 21586  | <i>Smith 2845</i>                           | Guyana              |                       |
| <i>P. hirsutipetiolata</i> Mildbr.       | U 14494  | <i>de Bruyn 1546</i>                        | Colombia            | 12                    |
| <i>P. hispida</i> Standl.                | U 25420  | <i>Cuatrecasas 14881</i>                    | Colombia, Choco     | 2                     |
| <i>P. lævis</i> Benth.                   | U 17502  | <i>Maguire &amp; al. 55576</i>              | Surinam             | 17                    |
| <i>P. maroniensis</i> R. Ben.            | U 1233   | <i>Lanjouw &amp; Lindeman 432</i>           | Surinam             | 25                    |
| »  | U 21508  | <i>Smith 2731</i>                           | Guyana              |                       |
| <i>P. melinonii</i> R. Ben.              | U 1208   | <i>Lanjouw &amp; Lindeman 399</i>           | Surinam             | 15                    |
| »  | U 20897  | <i>Prance &amp; Berg P 18136</i>            | Brasil, Amazonas    | 25                    |
| <i>P. mollis</i> Trec.                   | U 8669   | <i>Ellenberg 2297</i>                       | Peru                |                       |
| <i>P. ovata</i> Trec.                    | U 8155   | <i>Krukoff 7073</i>                         | Brasil, Amazonas    | 10                    |
| <i>P. substrigosa</i> Mildbr.            | Dw 5636  | <i>USw 6268</i>                             | Brasil              | 10                    |
| <i>P. triloba</i> Trec.                  | U 19886  | <i>Krukoff 5309</i>                         | Brasil, Acre        | 13                    |
| <i>P. sp.</i>                            | U 27206  | <i>Mexia s.n.</i>                           | Peru                |                       |
| <i>P. sp.</i>                            | U 27513  | <i>Dusén 17345</i>                          | Brasil, Parana      | 1,5                   |
| URTICACEÆ                                |          |   |                     |                       |
| <i>Boehmeria pavonii</i> Wedd.           | U 21090  | <i>Schunke 4977</i>                         | Peru                | 2                     |
| <i>B. ramiflora</i> Jacq.                | U 15446  | <i>Chambers 2686</i>                        | Dominica            | 4                     |
| <i>Gyrotænia microcarpa</i> F. & R.      | U 8357   | <i>USw 6019</i>                             | Jamaica             | 2                     |
| <i>Myriocarpa stipitata</i> Benth.       | U 21084  | <i>Schunke 4008</i>                         | Peru                | 1,5                   |
| <i>Touchardia latifolia</i> Gan.         | U 18601  | <i>Stern &amp; Herbst 518</i>               | Hawaii              | 4                     |
| <i>Urera elata</i> (Sw.) Griseb.         | U 27194  | <i>Mathias &amp; Taylor 5343</i>            | Peru                | 1                     |
| <i>U. hypselodendron</i> (Horhst.) Wedd. | U 15936  | <i>Schlieben 1721 ex RBHw</i>               | East Africa         | 3                     |
| »  | U 27404  | <i>Berg</i>                                 | Zimbabwe            | 3                     |

The quantitative wood data were measured as follows : vessel diameters were measured in tangential direction ; averages are based on 25 measurements. The vessel frequency is based on 25 counts of areas of 1 sq. mm. In the descriptions, average, minimum and maximum values are given for both characters. The percentage of solitary vessels was calculated after examining an area showing at least 100 pores. Clusters and multiples were regarded as 2, 3, 4, etc. vessels, depending on the number of vessels per group. For the intervacular pits the minimum and maximum sizes are given. Vessel member length, fibre length and parenchyma length (including both strands and fusiform cells) are based on 25 measurements per sample. Averages, minimum and maximum sizes are given. Additionally, the averages were used to calculate the ratio of fibre length/vessel element length, in the descriptions referred to as F/V ratio. For the fibres, maximum wall thickness, maximum lumen diameter and the average ratio of lumen diameter/wall thickness (= twice maximum wall thickness), in the descriptions referred to as L/W ratio, are given. Multiseriate ray height is presented in micrometers ( $\mu\text{m}$ ), ray width in number of cells. The data concern the averages of the 25 highest rays as observed in each section. Uniseriate ray height is based on 25 measurements per section. The percentage of uniseriate rays taken from the total number of uniseriate and multiseriate rays, and the percentage of vertically compound multiseriate rays is reported. The number of rays per mm is the average of 25 counts. The epidermal cells of the leaves as seen in the greater part of the samples were hardly measurable (e.g. covered by arachnoid hairs). In the descriptions the average dimensions of the epidermal cells are called tall (35—45  $\mu\text{m}$ ), small 25—35  $\mu\text{m}$ ), or very small (less than 25  $\mu\text{m}$ ). The shape of the periclinal walls is only mentioned if it is not straight or faintly sinusoid. "Intermediate layers" are layers of palisade-like tissue, consisting of conjugated spongy cells, lying between the palisade tissue and the spongy tissue. The midrib vascular system was studied at one third the lamina length from the leaf base. The petiole vascular system was studied at one half the length of the petiole.

## GENERIC DESCRIPTIONS

### I. SECONDARY XYLEM

#### 1. **Cecropia** Loefling — Pl. 2, 1.

Studied : 10 species, 19 specimens.

A genus of probably 70-80 species in tropical America, forming small to tall trees often with stilt-roots.

Growth rings faint or absent. Vessels diffuse, round to oval, solitary (50-82 %) and in radial multiples and irregular clusters of 2-3 (5), 1-3 (0-9) per sq. mm, diameter 155-300 (150-350)  $\mu\text{m}$ , vessel member length 500-690 (400-800)  $\mu\text{m}$ . Perforations simple. Intervascular pits alternate, round or polygonal, 12-18  $\mu\text{m}$ . Thin-walled tyloses present or absent.

Fibres non septate, diameter 26-50  $\mu\text{m}$ , walls 2-4 (6)  $\mu\text{m}$ , L/W ratio 1.6-10, gelatinous fibres scarce. Pits simple, mainly on the radial walls. Length 1100-2100 (975-2400)  $\mu\text{m}$ , F/V ratio 2.2-3.5.

Rays heterogeneous, uniseriate (3-25 %) and multiseriate, 3-7 (2-10) per mm, sheath cells scarcely present or absent. Uniseriate rays mainly composed of square to upright cells, ray height 300-700 (200-950)  $\mu\text{m}$ . Multiseriate rays composed of upright and procumbent cells, vertically compound 0-27 %, 1000-2200 (500-3250)  $\mu\text{m}$  high, 2-6 cells in width, uniseriate parts 1-4 (0-16) cells, sometimes containing rhombic crystals.

Parenchyma scarce. Paratracheal parenchyma vasicentric to aliform, sometimes confluent. Strands 4-6 (8) cells, length 570-770 (510-870)  $\mu\text{m}$ , sometimes containing rhombic crystals. Apotracheal parenchyma terminal, sometimes consisting of 2 narrow, concentric bands, present or absent.

Specific gravity : 0.25-0.55.

NOTE : Radial latex tubes were observed in a few samples of *C. sciadophylla* Mart. and in *C. monostachya* C. C. Berg.

## 2. *Coussapoa* Aublet — Pl. 2, 3.

Studied : 8 species 9 specimens.

A genus of 49 species in tropical America. Usually hemi-epiphytic shrubs or trees with aerial roots or with stilt-roots if terrestrial.

Growth rings faint or absent. Vessels diffuse, round to oval, solitary (25-83 %) and in radial multiples and irregular clusters of 2-8 (21), 1-6 (0-11) per sq. mm, diameter 220-300 (200-340)  $\mu\text{m}$ . Vessel member length 475-600 (400-725)  $\mu\text{m}$ . Perforations simple. Intervascular pits alternate, round or polygonal, 10-15  $\mu\text{m}$ . Thin-walled tyloses usually present.

Fibres non septate, diameter 18-25  $\mu\text{m}$ , walls 2-3.5  $\mu\text{m}$ , L/W ratio 2-5, gelatinous fibres usually present. Pits simple, mainly on the radial walls. Length 1100-1800 (875-2175)  $\mu\text{m}$ , F/V ratio 2.5-3.7.

Rays heterogeneous, uniseriate (21-35 %) and multiseriate, 4-7 (3-9) per mm, sheath cells present or absent. Uniseriate rays mainly composed of square to upright cells, ray height 300-500 (200-980)  $\mu\text{m}$ . Multiseriate rays composed of upright and procumbent cells, vertically compound 0-10 %, 700-1100 (450-1600)  $\mu\text{m}$  high, 3-6 cells in width, uniseriate parts 1-2 (0-8) cells.

Parenchyma paratracheal, banded, irregular, wavy, 1-2 (0-3) per mm, 5-9 (3-15) cells in width. Strands 5-8 (14) cells, length 600-710 (530-870)  $\mu\text{m}$ , containing some to many rhombic crystals.

Specific gravity : 0.50-0.75.

NOTE : Radial latex tubes observed in *C. latifolia* Aublet.

## 3. *Musanga* R. Brown — Pl. 2, 2.

Studied : 2 species, 10 specimens.

A genus of 2 species in tropical Africa forming trees with stilt-roots.

Growth rings faint or absent. Vessels diffuse, round to oval, solitary (50-93 %) and in radial multiples and irregular clusters of 2-3 (4), 1-2 (0-4) per sq. mm, diameter 210-310 (190-350)  $\mu\text{m}$ , vessel member length 450-605 (350-725)  $\mu\text{m}$ . Perforations simple. Intervascular pits alternate, round to polygonal, 12-15 (18)  $\mu\text{m}$ . Thin-walled tyloses usually present.



Fibres non septate, diameter 34-54  $\mu\text{m}$ , walls 1-3.5  $\mu\text{m}$ , L/W ratio 5-over 25, gelatinous fibres present or absent. Pits simple, mainly on the radial walls. Length 1150-1950 (975-2400)  $\mu\text{m}$ , F/V ratio 2.1-3.2.

Rays heterogeneous, uniseriate (5-11 (23) %) and multiseriate, 3-5 (2-7) per mm, sheath cells absent. Uniseriate rays mainly composed of square to upright cells, ray height 270-470 (200-720)  $\mu\text{m}$ . Multiseriate rays composed of upright and procumbent cells, vertically compound 0-60 %, 750-1100 (500-1850)  $\mu\text{m}$  high, 2-4 cells in width, uniseriate parts 1-3 (0-9) cells, often containing rhombic crystals.

Parenchyma scarce. Paratracheal parenchyma vasicentric to aliform, strands 4-5 (12) cells, length 625-775 (550-950)  $\mu\text{m}$ , often containing rhombic crystals. Apotracheal parenchyma terminal, present or absent.

Specific gravity : 0.12-0.40.

#### 4. **Myrianthus** Pal. Beauv. — Pl. 2, 4.

Studied : 4 species, 13 specimens.

A genus or 7 species in tropical Africa. Usually medium-sized trees or shrubs with stilt-roots or sometimes lianas.

Growth rings faint or absent. Vessels diffuse, round to oval, solitary (30-85 %) and in radial multiples and irregular clusters of 2-3 (5), 2-6 (1-11) per sq. mm, diameter 120-250 (110-275)  $\mu\text{m}$ , vessel member length 400-550 (300-675)  $\mu\text{m}$ . Perforations simple. Intervascular pits alternate, round or polygonal, 10-15  $\mu\text{m}$ . Thin-walled tyloses present or absent.

Fibres non septate, diameter 18-29  $\mu\text{m}$ , walls 2.2-5  $\mu\text{m}$ , L/W ratio 2-5, gelatinous fibres present or absent. Pits simple mainly on the radial walls. Length 1100-1850 (950-2125)  $\mu\text{m}$ , F/V ratio 2.5-4.0.

Rays heterogeneous, uniseriate (12-50 %) and multiseriate, 4-8 (2-10) per mm, sheath cells present or absent. Uniseriate rays mainly composed of square to upright cells, ray height 350-850 (250-1450)  $\mu\text{m}$ , multiseriate rays composed of upright and procumbent cells, vertically compound 0-10 %, 1000-1750 (700-2500)  $\mu\text{m}$ , 4-10 cells in width, uniseriate parts 1-4 (0-15) cells, sometimes containing rhombic crystals.

Parenchyma banded, irregular, wavy, 1-2 (3) per mm, 4-12 (3-16) cells in width. Strands 4-5 cells, length 420-670 (400-900)  $\mu\text{m}$ , containing some to many rhombic crystals.

Specific gravity 0.45-0.60.

#### 5. **Poikilospermum** Zipp. ex Miquel — Pl. 3, 1.

Studied : 4 species, 7 specimens.

A genus of 20 species in tropical Asia. Hemi-epiphytic scramblers with aerial roots.

Growth rings absent. Vessels diffuse, round to oval, solitary (55-88 %) and in radial multiples and irregular clusters of 2-3 (9), 5-9 (3-12) per sq. mm, diameter 260-310 (180-400)  $\mu\text{m}$ , vessel member length 325-385 (250-475)  $\mu\text{m}$ . Perforations simple. Intervascular pits alternate, round or polygonal, 15-20  $\mu\text{m}$ . Thin-walled tyloses present or absent.

Fibres showing dimorphism : short fibres, length 545-865 (400-1100)  $\mu\text{m}$ , non septate, diameter 22-26  $\mu\text{m}$ , walls 2.5-3.5  $\mu\text{m}$ , L/W ratio, 3.5-5, gelatinous fibres scarce. Pits simple, on radial and tangential walls. F/V ratio 1.6-2.4. Very long fibres, length 4000-5000  $\mu\text{m}$ .

Rays heterogeneous, multiseriate, partly unligified, composed of upright and procumbent cells, sometimes vertically compound to vertical rows, 1540-2875 (700-4700)  $\mu\text{m}$  high, 4-9 cells in width, uniseriate parts absent, 1-3 per mm.

Parenchyma : paratracheal parenchyma vasicentric ; apotracheal parenchyma in irregular unligified concentric bands. Strands 370-450 (275-625)  $\mu\text{m}$ , containing druses and often rhombic crystals.

Specific gravity unknown.

NOTE : Juvenile parts differ in many characters from the foregoing generic description :

Vessels 9-22 (3-33) per sq. mm, diameter 100-150 (85-200)  $\mu\text{m}$ , vessel member length 295-345 (200-450)  $\mu\text{m}$ .

Fibres, diameter 14-16  $\mu\text{m}$ , walls 3-4  $\mu\text{m}$ , L/W ratio 2-3. Very long fibres absent.

Rays heterogeneous or homogeneous, unligified parts scarce or absent, 4 (2-7) per mm.

Unligified apotracheal parenchyma absent or scarce.

## 6. **Pourouma** Aublet

Studied : 17 species, 26 specimens.

A genus of probably more than 50 species in tropical America. Small or medium-sized trees, often with stilt-roots.

Growth rings faint or absent. Vessels diffuse, round to oval, solitary (55-95 %) and in radial multiples and irregular clusters of 2-3 (4), 1-6 (0-8) per sq. mm, diameter 125-255 (110-305)  $\mu\text{m}$ , vessel member length 475-850 (350-930)  $\mu\text{m}$ . Perforations simple. Intervascular pits alternate, round or polygonal, 10-20  $\mu\text{m}$ . Thin-walled tyloses present or absent.

Fibres non septate, diameter 18-36  $\mu\text{m}$ , walls 1.2-4  $\mu\text{m}$ , L/W ratio 3-9, gelatinous fibres present or absent. Pits simple, mainly on the radial walls. Length 940-1725 (775-2 070)  $\mu\text{m}$ , F/V ratio 1.6-2.7.

Rays heterogeneous, uniseriate (5-53 %) and multiseriate, 4-9 (3-12) per mm, sheath cells present or absent. Uniseriate rays mainly composed of square to upright cells, ray height 300-750 (200-1000)  $\mu\text{m}$ , multiseriate rays composed of upright and procumbent cells, vertically compound 8-23 (45 %), 450-1260 (1800)  $\mu\text{m}$  high, 2-5 cells in width, uniseriate parts 1-6 (0-16) cells, sometimes containing rhombic crystals.

Parenchyma paratracheal variable, vasicentric and aliform to confluent and even banded. Bands irregular, wavy, 2-3 per mm, 5-6 (4-8) cells in width. Strands 5-6 (7) cells, length 560-950 (450-1000)  $\mu\text{m}$ , often containing rhombic crystals. Apotracheal parenchyma terminal, sometimes consisting of 2 narrow, concentric bands, present or absent.

Specific gravity 0.40-0.75.

NOTE : Radial latex tubes observed in one sample of *P. melinonii* R. Ben. The multi-seriate rays of *P. triloba* Trec. are much higher than those in the foregoing description : 2280 (1500-3500)  $\mu\text{m}$ .

### Discussion on wood anatomical characters

The family *Cecropiaceæ* can be divided into two groups : the genus *Poikilospermum* and the genera *Cecropia*, *Musanga*, *Coussapoa*, *Myrianthus* and *Pourouma*. The latter group can be sub-divided into the *Cecropia-Musanga* group and the *Coussapoa-Myrianthus* group, with *Pourouma* overlapping both groups. These divisions can be made with regard to many wood characteristics, for example (see also table 6) : the average number of vessels per sq. mm, 1-3 in *Cecropia* and *Musanga*, 1-6 in *Coussapoa*, *Myrianthus* and *Pourouma*, 5-9 in *Poikilospermum* ; the average vessel member length, 325-385  $\mu\text{m}$  in *Poikilospermum* and 400-850  $\mu\text{m}$  in the other genera ; the location of the fibre pits which are on both radial and tangential walls in *Poikilospermum* and on radial walls only in the other genera ; the average fibre length, 545-865  $\mu\text{m}$  for the short fibres and 4000-5000  $\mu\text{m}$  for the long fibres in *Poikilospermum* varies between 940 and 2100  $\mu\text{m}$  in the other genera ; the rays with exception of *Poikilospermum* consist of 2 types, uniseriates (5-53 %) and multiseriates ; the number of rays per mm, 1-3 in *Poikilospermum* and 3-9 in the other genera ; *Poikilospermum* is the only genus with unligified ray parts and unligified apotracheal parenchyma ; the average parenchyma strand length, 370-450  $\mu\text{m}$  in *Poikilospermum* and 420-950  $\mu\text{m}$  in the other genera ; the crystal type, druses and rhombic crystals in *Poikilospermum* and rhombic crystals only in the other genera.

The genus *Poikilospermum* consists of hemi-epiphytic scramblers. The unligified parenchyma and the reticulate parenchyma pattern in this genus might be related to the climbing habit (TER WELLE & KOEK-NOORMAN, 1981). Because of the facts that there are non-climbing members of the *Urticaceæ* which also have unligified parts and that all (climbing) members of the *Moraceæ* lack this phenomenon, this character supports the taxonomic separation of *Poikilospermum* from the other genera. Species of the genus *Coussapoa* are usually hemi-epiphytic. The only indication of a correlation between this habit and the characters found might be the number of vessels per multiple, which is also observed in the hemi-epiphytic genus *Poikilospermum*. *Pourouma* and *Myrianthus* are small to medium-sized trees, *Cecropia* and *Musanga* are pioneer plants (BERG, 1978, 1981). These two groups of genera show similarities in characters. The montane species like *Myrianthus holstii* Engl. and *Musanga leo-errerae* Haum. show a smaller pore and fibre diameter, and shorter vessel members and fibres than the lowland species like *Myrianthus arboreus* Pal. Beauv. and *Musanga cecropioides* R. Br. (cf. VAN DEN OEVER, BAAS & ZANDEE, 1981).

Considering the range of diversity of the wood characters of the *Moraceæ*, the *Cecropiaceæ* could be placed in the *Moraceæ* on the basis of their wood structure (MENNEGA, pers. comm. in BERG, 1978 ; TOPPER, pers. comm.). This may be true concerning the genera *Cecropia*, *Coussapoa*, *Musanga*, *Myrianthus* and *Pourouma*, particularly because of the presence of latex tubes in some samples. These 5 genera are characterized by diffusely distributed vessels, solitary (25-95 %) and in radial multiples and irregular clusters of 2-8 (21), 1-6 (0-11) per sq. mm, diameter 120-310 (110-350)  $\mu\text{m}$ , vessel member length 400-850 (300-930)  $\mu\text{m}$ .

Perforations simple. Intervascular pits alternate, round or polygonal, 10-18  $\mu\text{m}$ . Fibres non septate, diameter 18-54  $\mu\text{m}$ , walls 1-5 (6)  $\mu\text{m}$ , L/W ratio 1.6-over 25. Pits simple, on radial walls. Length 940-2100 (775-2400)  $\mu\text{m}$ , F/V ratio 1.6-4.0. Rays heterogeneous, uniseriate (0-53 %) and multiseriate, 3-9 (2-12) per mm. Uniseriate rays mainly composed of square to upright cells, ray height 270-850 (200-1450)  $\mu\text{m}$ . Multiseriate rays composed of upright and procumbent cells, vertically compound 0-60 %, 450-2200 (350-3250)  $\mu\text{m}$  high, 2-10 cells in width, uniseriate parts 1-6 (16) cells. Paratracheal parenchyma vasicentric, aliform, confluent or banded; bands irregular, wavy, 1-3 per mm, 4-12 (3-16) cells in width. Strands 420-950 (400-1000)  $\mu\text{m}$ , 3-8 (4-11) cells, often containing rhombic crystals. Specific gravity 0.12-0.75.

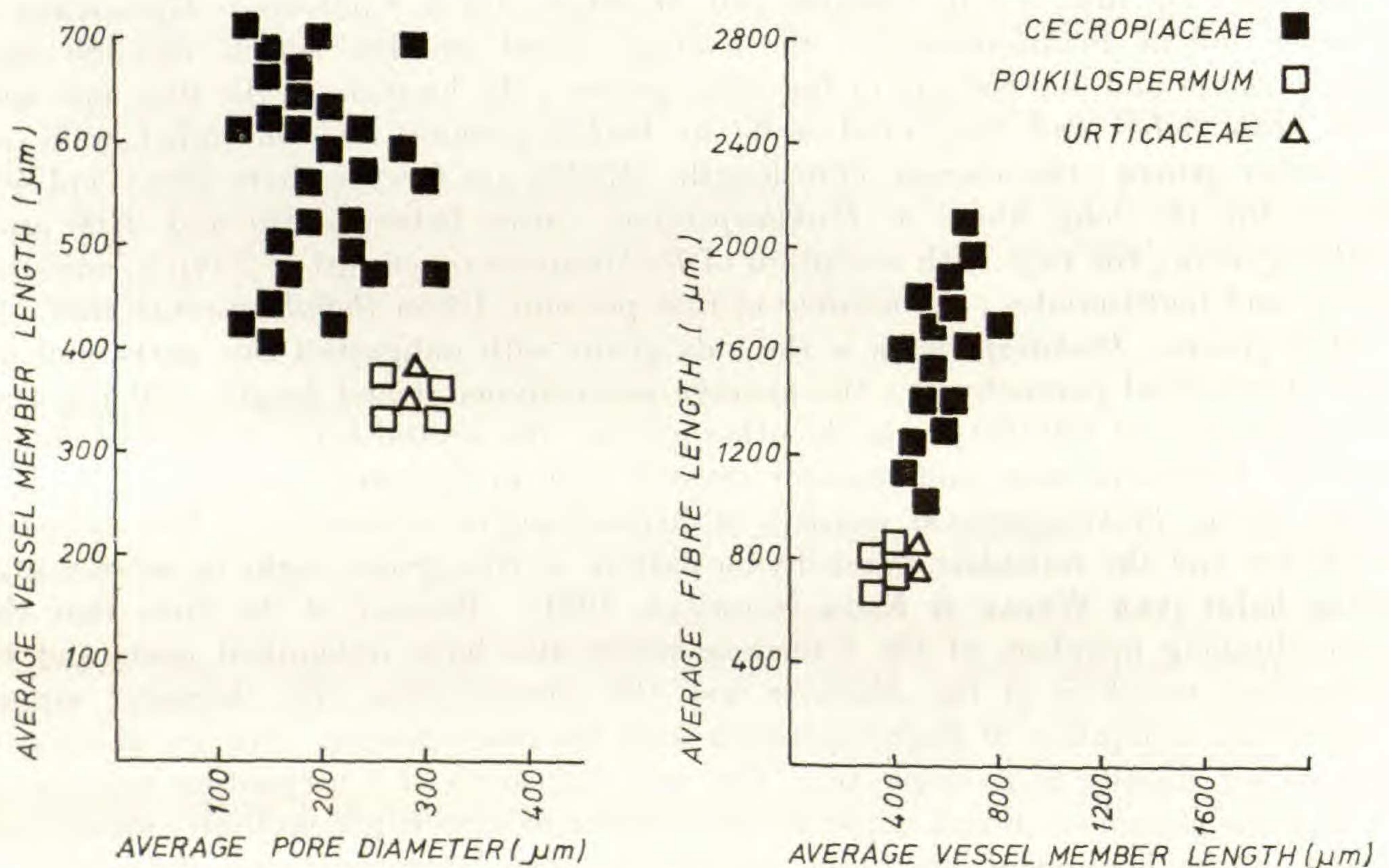


FIG. 1. — Vessel member length, fibre length, and pore diameter of the *Cecropiaceae*, the genus *Poikilospermum* and some representatives of the *Urticaceae*.

Based on data from literature (METCALFE & CHALK, 1950) and on our own observation the wood of *Poikilospermum* seems to be rather urticaceous. Its vessel diameter, F/V-ratio (see fig. 1), location of the fibre pits, ray type, number of rays per mm, the presence of unignified parts, and the crystal type are in agreement with features observed in species of the genera *Boehmeria*, *Gyrotænia*, *Myriocarpa*, *Touchardia*, *Urera* and *Urtica*. The presence of the 4000-5000 mm long fibres which occur in *Poikilospermum* could not be demonstrated in the *Urticaceae*. Some of the species of the tribes *Urereæ* and *Boehmerieæ* have unignified parenchyma in the wood, part of these species are climbers or lianas (e.g. *Urera hypselodendron*, Pl. 3,2), the others are non-climbing shrubs or herbs (e.g.

*Gyrotænia*, *Laportea*, *Myriocarpa*, *Touchardia*, *Urtica dioica*, *Urera elata*). Table 3 shows that the wood of *Poikilospermum* closely resembles the wood of the climbing representatives of the tribe *Urereæ*.

TABLE 3 : Comparison of relevant characters of the genus *Poikilospermum* and some urticaceous taxa.

|  | U. hyps.<br>(A) | Poik.<br>(A) | Poik.<br>(J) | U. hyps.<br>(J) | Boehmeria | Urticaceæ |
|--|-----------------|--------------|--------------|-----------------|-----------|-----------|
| Vessel diameter ( $\mu\text{m}$ )      | 290-350         | 260-310      | 100-150      | 120-180         | 90-120    | 110-140   |
| Vessel member length ( $\mu\text{m}$ ) | 375             | 325-385      | 295-345      |                 | 330-475   | 445-520   |
| Vessels per sq. mm                     | 4-10            | 5-9          | 9-22         | 8-12            | 17-23     | 8-16      |
| Fibre length ( $\mu\text{m}$ )         | 630-810         | 550-870      | 655-810      |                 | 650-730   | 725-920   |
| Fibre pit location                     | R, T            | R, T         | R, T         | R, T            | R, T      | R, T      |
| Rays per mm                            | 1-3             | 1-3          | 2-7          | 2-6             | 5-8       | 2-6       |
| Unlignified parts                      | +               | +            | —            | —               | —         | +         |
| Druses                                 | +               | +            | +            | +               | +         | +         |

U. hyps. = *Urera hypselodendron*; Poik. = *Poikilospermum*; A = adult; J = juvenile; *Urticaceæ* = the non-climbing species with unlignified parts in the wood.

TABLE 4 : Comparison of relevant characters of the climbing species of the tribe *Urereæ*, the genus *Poikilospermum*, the *Cecropiaceæ* s. s. (containing the genera *Cecropia*, *Coussapoa*, *Musanga*, *Myrianthus* and *Pourouma*) and the *Moraceæ* (METCALFE & CHALK, 1950; TOPPER, pers. comm.) and the *Urticaceæ* (METCALFE & CHALK, 1950; GANGADHARA & INAMDAR, 1977).

| WOOD                                   | URTICACEÆ   | UREREÆ    | POIKILOSP. | CECR. s.s. | MORACEÆ   |
|--|-------------|-----------|------------|------------|-----------|
| Vessel diameter ( $\mu\text{m}$ )      | 100-200     | 290-350   | 260-310    | 120-310    | 100-200   |
| Vessel member length ( $\mu\text{m}$ ) | 300-500     | 375       | 325-385    | 400-850    | 300-500   |
| Vessels per sq. mm                     | 1-6(15)     | 4-10      | 5-9        | 1-6        | 1-5       |
| Fibre length ( $\mu\text{m}$ )         | 750-1500    | 630-810   | 550-870    | 940-2100   | 600-1900  |
| Fibre pit location                     | R, T        | R, T      | R, T       | R          | R         |
| Ray type (Kribs, 1935)                 | He I, Ho II | Ho II     | Ho II      | He II      | He I, II  |
| Rays per mm                            | 1-3         | 1-3       | 1-3        | 3-9        | 3-11      |
| Unlignified parts                      | +/-         | +         | +          | —          | —         |
| Druses                                 | +/-         | +         | +          | —          | —         |
| LEAF                                   |             |           |            |            |           |
| Stomatal type                          | ani-ano     | ani (ano) | ani        | ano        | ano (ani) |
| Bundle sheath extensions               | —           | —         | —          | +          | +         |
| Long shaped cystoliths                 | +/-         | +         | +          | —          | —         |
| Raphides                               | +/-         | +/-       | +/-        | —          | —         |

Stomatal types : ano = anomocytic; ani = anisocytic (METCALFE & CHALK, 1979).

## II. LEAF ANATOMICAL DESCRIPTIONS

### 1. *Cecropia* Loefling — Pl. 4, 2, 3.

Studied : 4 species, 5 specimens.

**IN SURFACE VIEW :** Indumentum of thin, frizzed, unicellular, arachnoid hairs, abaxial ; unicellular, needle-shaped, rarely hooked hairs (mainly on abaxial surface, rarely also on adaxial surface) ; adaxial, glandular hairs with multicellular, globular heads on 3-5-celled, uniseriate stalks, solitary or in groups of 2-4 ; abaxial, uniseriate 5-8-celled, curved, glandular hairs with or without globular to elongated heads ; and mostly abundant, conical papillae containing lithocysts. Müllerian bodies and pearl glands present or absent. Epidermal cells polygonal ; adaxial cells overlying large crystalliferous mesophyll cells forming a rosette. Stomata almost entirely confined to abaxial surface, anomocytic, average length of guard cell pairs 15-20  $\mu\text{m}$ , average width 12-18  $\mu\text{m}$ . Hydathodes formed by 10-15 water pores each, present or absent on adaxial surface. Minor veins usually very prominent in abaxial epidermis.

**IN TRANSVERSE SECTION :** Lamina bifacial. Epidermal cells small, especially abaxially between the veins. Adaxial epidermal cells sometimes with periclinal division walls and/or mucilaginous inner walls. Stomata raised above level of unspecialized cells. Adaxial hypodermis of 1 or 2 layers of parenchyma cells, including mucilage cells present or absent. Mesophyll consisting of one layer of palisade cells (sometimes subdivided), compact spongy tissue, with or without an intermediate layer in between. Veins with sclerenchymatous vertical bundle sheath extensions (touching adaxial hypodermis and abaxial epidermis). Midrib with a flat or raised adaxial surface and a prominently raised abaxial surface ; peripheral ground tissue parenchymatous to collenchymatous, interspersed with mucilage cells ; vascular system composed of a closed or variously interrupted cylinder, partly or wholly surrounded by sclerenchyma fibres, and enclosing a parenchymatous " pith ". Vascular system of petiole similar. Crystals present as large druses throughout mesophyll and as small to large druses in petiole and midrib.

**NOTE :** Müllerian bodies (SCHIMPER, 1888 ; RICKSON, 1971, 1976) are ovoid or pear-shaped,  $3 \times 1$  mm, deciduous, multicellular, food bodies. The apex of each body communicates with the exterior via a stoma (METCALFE & CHALK, 1950). The bodies on the lower surface of the base of the petiole are situated amongst a velvety covering of uniseriate hairs (BAILY, 1922 ; JANZEN, 1973). Sometimes these trichilia are reduced or even lacking (BERG, 1980, 1981 ; BURGER, 1977).

Pearl glands (MEYEN, 1837) are trichomes on the petiole and the blade. They are non-secretory, large, vacuolate cells, containing lipid droplets and a small number of glycogen plastids (RICKSON, 1976).

## 2. *Coussapoa* Aublet

Studied : 11 species, 18 specimens.

**IN SURFACE VIEW :** Indument of thin, frizzed, unicellular arachnoid hairs, abaxially present or absent ; unicellular needle-shaped, often wavy hairs (mostly on abaxial surface, rarely also on adaxial surface) ; adaxial, glandular hairs with multicellular, globular heads on 3-5-celled, uniseriate stalks, mostly in groups of 2-4, present or absent ; abaxial, uniseriate, 6-10-celled, curved, glandular hairs with globular to elongated heads, mostly present ; and conical papillæ sometimes present. Epidermal cells polygonal ; adaxial cells overlying large crystalliferous mesophyll cells forming a rosette. Stomata confined to abaxial surface, anomocytic, average length of guard cell pairs 15-20  $\mu\text{m}$ , average width 12-18  $\mu\text{m}$ . Hydathodes formed by 10-15 water pores each, present or absent on adaxial surface. Minor veins usually very prominent in abaxial epidermis.

**IN TRANSVERSE SECTION :** Lamina bifacial. Epidermal cells small, especially abaxially between the veins. Adaxial epidermal cells sometimes with silicified outer walls. Stomata sometimes raised above level of unspecialized cells. Adaxial hypodermis of 2 or 3 layers of parenchyma cells, including mucilage cells except in *C. villosa*. Mesophyll consisting of one layer of palisade cells (sometimes subdivided), loose spongy tissue, with or without an intermediate layer in between. Veins with sclerenchymatous vertical bundle sheath extensions (touching adaxial hypodermis and abaxial epidermis). Midrib with a flat or raised adaxial surface and a prominently raised abaxial surface ; peripheral ground tissue parenchymatous to collenchymatous, interspersed with mucilage cells ; vascular system composed of a closed or variously interrupted cylinder, partly or wholly surrounded by sclerenchyma fibres, and enclosing 1 or 2 rows of bundles which are situated in the same direction as the most abaxial bundle of the cylinder (Pl. 1, 3). Vascular system of petiole similar. Crystals present as druses throughout the mesophyll, in petiole and midrib ; rhombic crystals sometimes present.

## 3. *Musanga* R. Brown

Studied : 1 species, 2 specimens.

**IN SURFACE VIEW :** Indumentum of thin, frizzed, unicellular arachnoid hairs, abaxial ; unicellular needle-shaped hairs on abaxial surface ; adaxial, glandular hairs with multicellular, globular heads on 3-5-celled, uniseriate stalks, in groups of 2-7 ; adaxial, uniseriate, 5-8-celled, curved, glandular hairs with or without globular to elongated heads ; and conical papillæ. Epidermal cells polygonal ; stomata entirely confined to abaxial surface, anomocytic, average length of guard cell pairs 15-20  $\mu\text{m}$ , average width 12-18  $\mu\text{m}$ . Minor veins usually very prominent in abaxial epidermis.

**IN TRANSVERSE SECTION :** Lamina bifacial. Epidermal cells small. Adaxial epidermal cells sometimes with silicified outer walls. Adaxial hypodermis of 2 layers of parenchyma

cells, including mucilage cells. Mesophyll consisting of one layer of palisade cells, compact spongy tissue, with or without an intermediate layer in between. Veins with parenchymatous to collenchymatous vertical bundle sheath extensions (touching adaxial hypodermis and abaxial epidermis). Midrib with grooved adaxial surface and prominently raised abaxial surface; peripheral ground tissue parenchymatous to collenchymatous, interspersed with mucilage cells; vascular system composed of a closed or variously interrupted cylinder, partly or wholly surrounded by sclerenchyma fibres, and enclosing a parenchymatous "pith". Vascular system of petiole similar. Crystals present as druses throughout mesophyll, in petiole and midrib; rhombic crystals sometimes present in midrib.

4. **Myrianthus** Pal. Beauv. — Pl. 4, 1.

Studied : 3 species, 3 specimens.

IN SURFACE VIEW : Indumentum of thin, frizzed, unicellular arachnoid hairs, abaxial; unicellular, sometimes bicellular, needle-shaped hairs (mainly on abaxial surface, rarely also on adaxial surface); adaxial, glandular hairs with multicellular, globular heads on 3-5-celled, uniseriate stalks, in groups of 2-7; abaxial, uniseriate, 5-8 celled, curved, glandular hairs with or without globular to elongated heads. Epidermal cells polygonal; abaxial cells partly papillated. Stomata entirely confined to abaxial surface, anomocytic, average length of guard cell pairs 15-20  $\mu\text{m}$ , average width 12-18  $\mu\text{m}$ . Minor veins usually very prominent in abaxial epidermis.

IN TRANSVERSE SECTION : Lamina bifacial. Epidermal cells small, especially abaxially between the veins. Adaxial hypodermis of 1 or 2 layers of parenchyma cells. Mesophyll consisting of one layer of palisade cells, compact spongy tissue, with or without an intermediate layer in between. Veins with sclerenchymous vertical bundle sheath extensions (touching adaxial hypodermis and abaxial epidermis). Midrib with a flat adaxial surface and prominently raised abaxial surface; peripheral ground tissue parenchymatous to collenchymatous, interspersed with mucilage cells; vascular system composed of a closed or variously interrupted cylinder, partly or wholly surrounded by sclerenchyma fibres, and enclosing 1 or 2 rows of bundles which are situated in the same direction as the most abaxial bundle of the cylinder (Pl. 1, 3). Vascular system of petiole composed of a closed cylinder. Crystals present as large druses throughout the mesophyll and as small to large druses and rhombic crystals in petiole and midrib.

5. **Poikilospermum** Zipp. ex Miquel — Pl. 3, 3, 4.

Studied : 4 species, 5 specimens.

IN SURFACE VIEW : Indumentum of unicellular, needle-shaped hairs sometimes on abaxial surface; abaxial and adaxial, glandular hairs with unicellular or uniseriate heads (shape varies in the different species) on unicellular stalks. Epidermal cells polygonal. Stomata confined to the abaxial side, anisocytic, average length of guard cell pairs 25-30  $\mu\text{m}$ ,



average width 20-25  $\mu\text{m}$ . Hydathodes formed by 20-40 water pores diffusely distributed on adaxial surface.

IN TRANSVERSE VIEW : Lamina bifacial. Epidermal cells tall. Abaxial epidermal cells sometimes with periclinal division walls. Adaxial hypodermis of 1, 2 or 3 layers of parenchyma cells, including mucilage cells. Mesophyll consisting of two layers of palisade cells, and loose spongy tissue. Midrib with a flat adaxial surface and a prominently raised abaxial surface ; peripheral ground tissue parenchymatous to collenchymatous, interspersed with mucilage cells ; vascular system composed of one or more parallel arcs, partly or wholly surrounded by sclerenchyma fibres ; the upper arc with strongly incurved edges. Vascular system of petiole composed of one or more closed or variously interrupted parallel arcs. Crystals present as numerous druses throughout mesophyll, in petiole and midrib ; raphides sometimes present in mesophyll. Cystoliths on both surfaces, on adaxial surface arranged pointing towards hydathodes (Pl. 3,4) and sometimes penetrating deeply into mesophyll, on abaxial surface along midrib and veins ; in shape punctiform, elongate or stellate.

#### 6. **Pourouma** Aublet — Pl. 4, 4.

Studied : 10 species, 12 specimens.

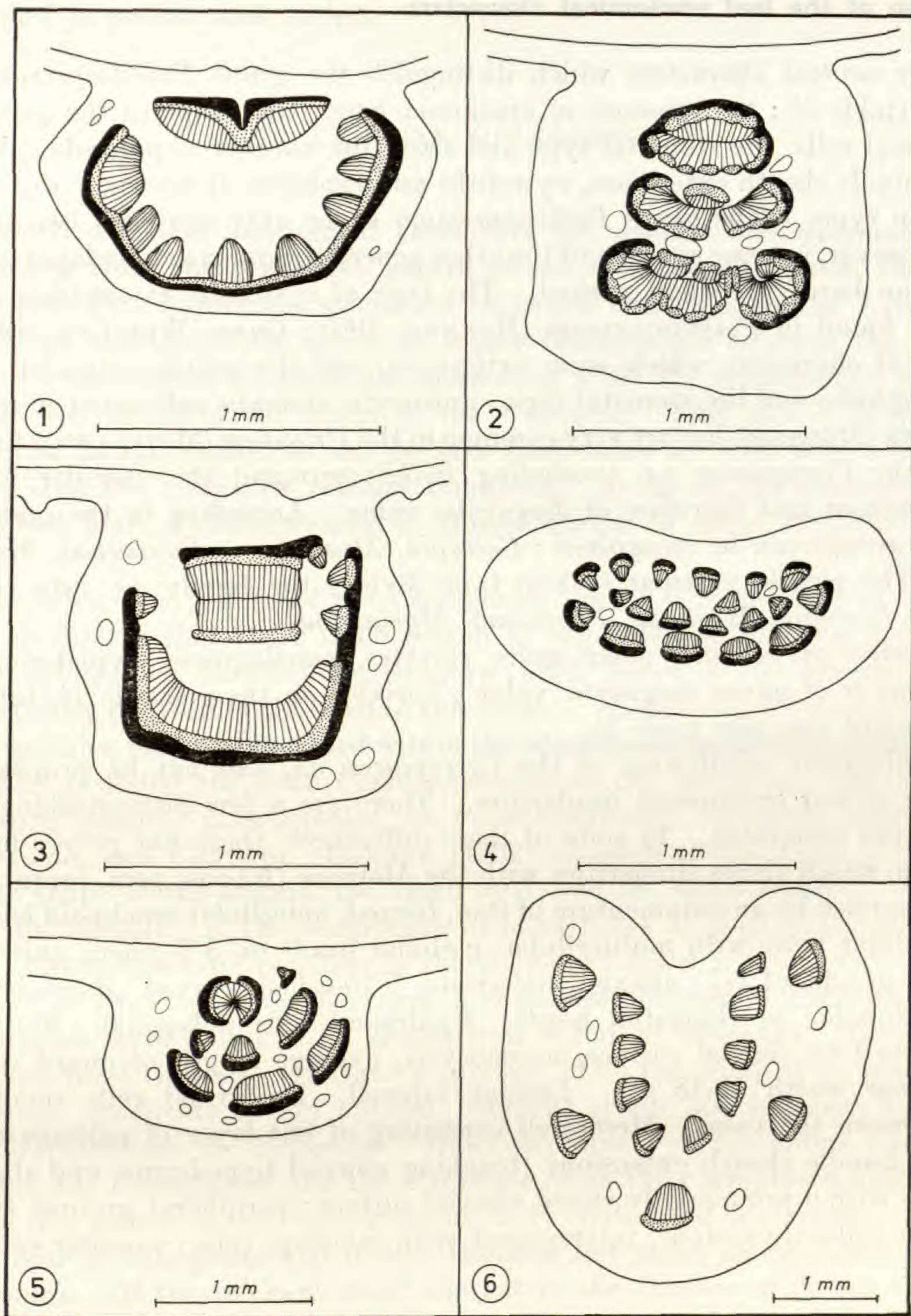
IN SURFACE VIEW : Indumentum of thin, frizzed, unicellular arachnoid hairs, abaxial ; unicellular needle-shaped hairs (on abaxial surface and sometimes on adaxial surface) ; adaxial, glandular hairs with multicellular, globular heads on 3-7-celled, uniseriate stalks, in groups of 2-7, often in pits ; abaxial, uniseriate, 5-8-celled, curved, glandular hairs with or without globular to elongated heads ; and conical papillæ, sometimes present. Epidermal cells polygonal ; abaxially rarely papillated ; adaxial cells overlying large crystalliferous mesophyll cells forming a rosette. Stomata entirely confined to abaxial surface, anomocytic, average length of guard cell pairs 15-20  $\mu\text{m}$ , average width 12-18  $\mu\text{m}$ . Hydathodes formed by 10-15 water pores each, sometimes present on adaxial surface. Minor veins very prominent in abaxial epidermis.

IN TRANSVERSE SECTION : Lamina bifacial. Epidermal cells small, especially between the veins. Stomata raised on pedestals. Adaxial hypodermis of 1 or 2 layers of parenchyma cells. Mesophyll consisting of one layer of palisade cells, loose or compact spongy tissue, with or without an intermediate layer in between. Veins with sclerenchymatous vertical bundle sheath extensions (touching adaxial hypodermis and abaxial epidermis). Midrib with a flat or grooved adaxial surface and a prominently raised abaxial surface ; peripheral ground tissue parenchymatous to collenchymatous, interspersed with mucilage cells ; vascular system composed of 2 or 3 closed or variously interrupted flattened cylinders, partly or wholly surrounded by sclerenchyma fibres (Pl. 1, 2). Vascular system of petiole composed of a closed or variously interrupted cylinder, partly or wholly surrounded by sclerenchyma fibres, and enclosing a parenchyma "pith". Crystals present as large druses throughout mesophyll ; sometimes druses in midrib, petiole and/or adaxial epidermis.

TABLE 5 : Comparison of some leaf anatomical characters of the *Cecropiaceæ s.l.*

|                                    | <i>Cecropia</i> | <i>Coussapoa</i> | <i>Musanga</i> | <i>Myrianthus</i> | <i>Pourouma</i> | <i>Poikilospermum</i> |
|------------------------------------|-----------------|------------------|----------------|-------------------|-----------------|-----------------------|
| <b>INDUMENTUM :</b>                |                 |                  |                |                   |                 |                       |
| arachnoid hairs                    | +               | +                | +              | +                 | +               | —                     |
| needle-shaped hairs                | +               | (+)              | +              | +                 | +               | (+)                   |
| conical papillae                   | +               | (+)              | —              | —                 | (+)             | —                     |
| similar glands on both surfaces    | —               | —                | —              | —                 | —               | +                     |
| <b>EPIDERMIS :</b>                 |                 |                  |                |                   |                 |                       |
| cell size                          | small           | small            | small          | small             | small           | large                 |
| silicified outer walls             | (+)             | (+)              | +              | —                 | —               | —                     |
| rosettes                           | (+)             | (+)              | (+)            | —                 | +               | —                     |
| <b>STOMATA :</b>                   |                 |                  |                |                   |                 |                       |
| type                               | anomocytic      | anomocytic       | anomocytic     | anomocytic        | anomocytic      | anisocytic            |
| size ( $\mu\text{m}$ )             | 15-20           | 15-20            | 15-20          | 15-20             | 15-20           | 25-30                 |
| raised                             | (+)             | (+)              | —              | —                 | +               | —                     |
| <b>HYDATHODES</b>                  | (+)             | (+)              | —              | —                 | (+)             | +                     |
| <b>HYPODERMIS :</b>                |                 |                  |                |                   |                 |                       |
| number of cell layers              | 0-2             | 2-3              | 2              | 1-2               | 1-2             | 1-3                   |
| mucilage cells                     | +               | (+)              | +              | —                 | —               | +                     |
| <b>MESOPHYLL :</b>                 |                 |                  |                |                   |                 |                       |
| number of palisade cell layers     | 1               | 1                | 1              | 1                 | 1               | 2                     |
| intermediate layer                 | (+)             | (+)              | —              | (+)               | (+)             | —                     |
| spongy tissue type                 | compact         | loose            | compact        | compact           | loose/compact   | loose                 |
| <b>BUNDLE SHEATH EXTENSIONS</b>    | +               | +                | +              | +                 | +               | —                     |
| <b>MIDRIB VASCULAR SYSTEM TYPE</b> | I               | II               | I              | II                | III             | plate 1, 5            |
| <b>PETIOLE VASC. SYSTEM TYPE</b>   | I               | II               | I              | I                 | I               | plate 1, 6            |
| <b>CRYSTAL TYPE</b>                | dr              | dr/rh            | dr/rh          | dr/rh             | dr              | dr/raphides           |
| <b>CYSTOLITHS IN LAMINA</b>        | —               | —                | —              | —                 | —               | +                     |

Legend : dr = druses, rh = rhombic crystals, (+) = absent or present.



Pl. 1. — *Cecropia latiloba* Miq. : 1, T. S. of the midrib. — *Pourouma laevis* Benth. : 2, T. S. of the midrib. — *Myrianthus serratus* (Trec.) B. & H. : 3, T. S. of the midrib. — *Coussapoa nitida* Miq. : 4, T. S. of the petiole. — *Poikilospermum inaequale* Chew : 5, T. S. of the midrib ; 6, T. S. of the petiole.

### Discussion of the leaf anatomical characters

There are several characters which distinguish the genus *Poikilospermum* from the other genera (table 5) : the presence of arachnoid hairs, the shape of the glands, the size of the epidermal cells, the stomatal type and sizes, the number of palisade cell layers, the presence of bundle sheath extensions, cystoliths and raphides (if present), and the vascular bundle system types. The genus *Poikilospermum* is the only one with two true palisade cell layers, however, in some samples of the other genera the intermediate layer is so palisade-like that it can hardly be distinguished. The type of cystoliths as occurring in the *Urticaceæ* can be found in *Poikilospermum* (RENNER, 1907 ; CHEW WEE-LEK, 1963). Other leaf anatomical characters which seem urticaceous are the petiole vascular system, the presence of raphides and the stomatal type : anisocytic stomata only occur in a part of the genus *Dorstenia* (*Moraceæ*), but are very common in the *Urticaceæ* (METCALFE & CHALK, 1950).

Within the *Cecropiaceæ s.s.* (excluding *Poikilospermum*) the vascular bundle types are rather constant and therefore of diagnostic value. According to the midrib vascular system three groups can be recognized : *Cecropia*, *Musanga* — *Coussapoa*, *Myrianthus* — *Pourouma*. The petiole vascular system type divides the family *s.s.* into two groups : *Coussapoa* — *Cecropia*, *Musanga*, *Pourouma*, *Myrianthus*.

The presence of silicified outer walls, rosettes, mucilaginous hypodermal cells and conical papillae is of minor diagnostic value : variable on the genus level, totally lacking or always present (see also table 5).

An unambiguous subdivision of the *Cecropiaceæ s.s.* can not be proposed, because of the degree of leaf anatomical similarities. There are a few distinguishing characters, but they are not correlated. In spite of these differences, these five genera form a homogeneous group, which shows similarities with the *Moraceæ* (KLOOS, pers. comm.) and which can be characterized by an indumentum of thin, frizzed, unicellular arachnoid hairs, abaxial ; adaxial, glandular hairs with multicellular, globular heads on 3-7-celled, uniseriate stalks, solitary or in groups of 2-7 ; abaxial, uniseriate, 5-10-celled, curved, glandular hairs with or without globular to elongated heads. Epidermal cells polygonal. Stomata almost entirely confined to abaxial surface, anomocytic, average length of guard cell pairs 15-20  $\mu\text{m}$ , average width 12-18  $\mu\text{m}$ . Lamina bifacial. Epidermal cells small, especially abaxially between the veins. Mesophyll consisting of one layer of palisade cells. Veins with vertical bundle sheath extensions (touching adaxial hypodermis and abaxial epidermis). Midrib with a prominently raised abaxial surface ; peripheral ground tissue parenchymatous to collenchymatous, interspersed with mucilage cells ; vascular system divided into 3 types :

I : a closed or variously interrupted cylinder, partly or wholly surrounded by sclerenchyma fibres, and enclosing a parenchymatous " pith " (Pl. 1, 1).

II : a closed or variously interrupted cylinder, partly or wholly surrounded by sclerenchyma fibres, and enclosing 1 or 2 rows of bundles which are situated in the same direction as the most abaxial bundle of the cylinder (Pl. 1, 3).

III : 2 or 3 closed or variously interrupted flattened cylinders, partly or wholly surrounded by sclerenchyma fibres (Pl. 1, 2).

Vascular system of petiole : type I or II. Crystals present as druses throughout mesophyll, and in petiole and midrib.

#### GENERAL DISCUSSION

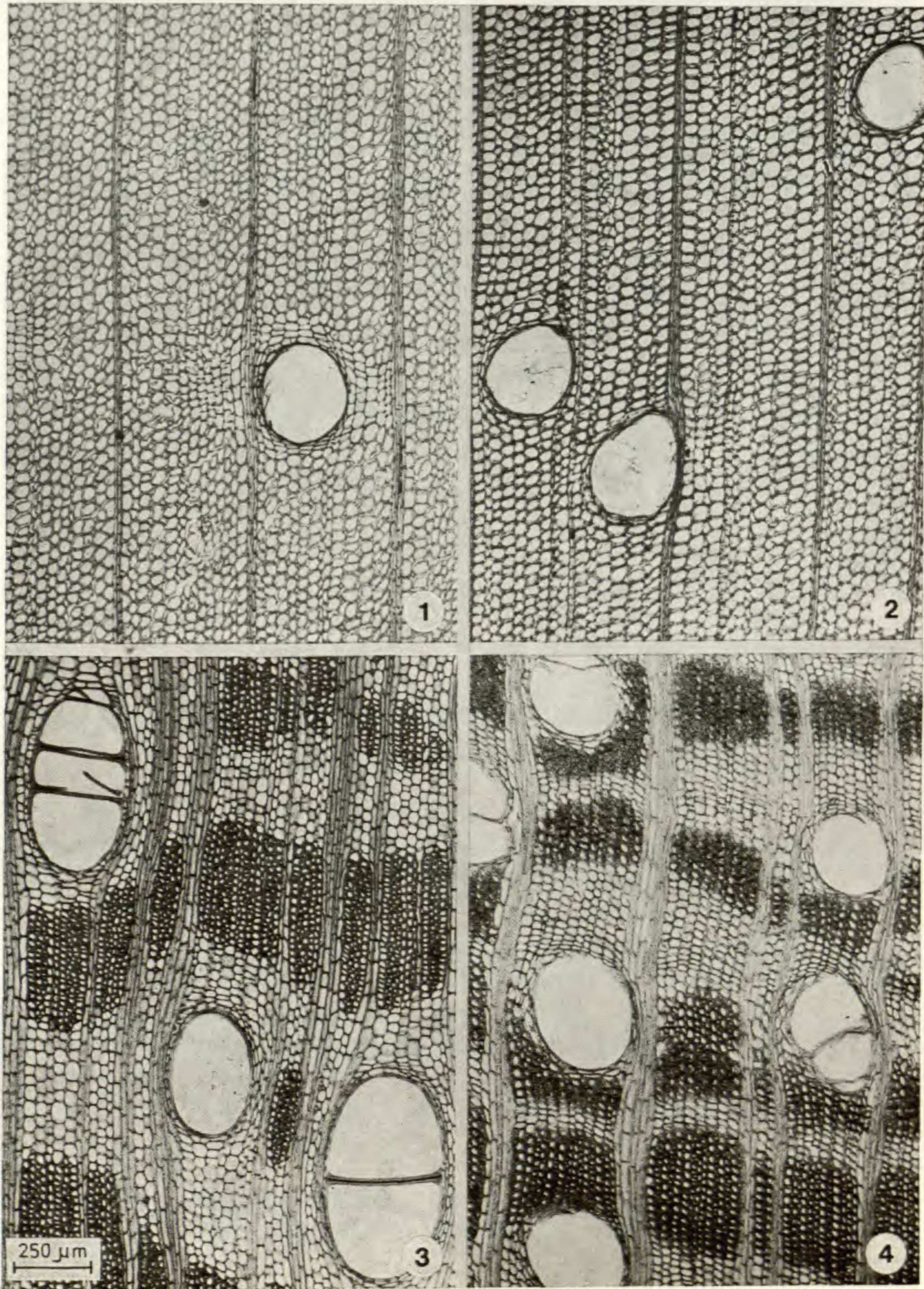
Using wood and leaf anatomical characters the genus *Poikilospermum* deviates in many characters from the other five genera of the *Cecropiaceæ*. From these data it is quite clear that *Poikilospermum* should be classified elsewhere in the *Urticales*. CHEW WEE-LEK (1963) considered the genus as rather intermediate between the *Moraceæ* and the *Urticaceæ* : the vegetative parts are moraceous while the reproductive parts are urticaceous. He has classified the genus in the *Urticaceæ*. This idea is supported by the results obtained in this study, as can be seen from table 4. The proper place of *Poikilospermum* within the *Urticaceæ* remains doubtful. As far as the anatomy of the *Urticaceæ* is studied here, *Poikilospermum* is almost similar in wood structure to the genus *Urera*.

The remaining five genera of the *Cecropiaceæ* are so homogeneous in wood and leaf anatomical characters that there is no reason to separate one of these genera from this group. The subdivision described by RENNER (1907) based on the adaxial glands, is not at all supported by the results obtained in this study. Should this wood and leaf anatomical rather homogeneous group be included within the *Moraceæ* or should it be given family rank? ENGLER (1889) included the tribe *Conocephaloideæ* in the *Moraceæ*. The tribe consisted of the following genera : *Conocephalus* (= *Poikilospermum*), *Musanga*, *Myrianthus*, *Coussapoa*, *Pourouma*, and *Cecropia*. CORNER (1962) transferred this tribe to the *Urticaceæ*, based on the shape of the stigma, the small seed, and the small embryo. One character not studied by himself, i.e. the occurrence of latex-tubes at least in the primary bark, is moraceous. Latex-tubes are common in the secondary wood of most genera of the *Moraceæ* but scarce in a few species of *Cecropia*, and possibly present in *Pourouma* and *Coussapoa*. Latex-tubes were found to be absent from wood of *Musanga*, *Myrianthus*, *Poikilospermum*, and the *Urticaceæ*. In BERG's opinion (1978) the group of six genera (including *Poikilospermum*) constitute a very natural, coherent group, which merits a rank equal to that of the *Moraceæ* and the *Urticaceæ*. However, almost all characters discussed by him occur in either the *Cecropiaceæ* and the *Urticaceæ* or in the *Cecropiaceæ* and the *Moraceæ*. The group of five genera is very homogeneous in its anatomical characters. Bundle sheath extensions occur in this group and in the *Moraceæ* but never in the *Urticaceæ* (including *Poikilospermum*). Of the relevant wood characters the absence of druses and unlignified parts, the number of rays per mm, the composition of the rays, and the location of the fibre pits restricted to the radial walls, are shared by the *Cecropiaceæ s.s.* and the *Moraceæ*. There are neither leaf nor wood anatomical characters that occur exclusively in the *Urticaceæ* and *Cecropiaceæ*, and not in the *Moraceæ*. These results are supported by the studies of the wood and the leaf anatomy of the family of the *Moraceæ*, S. M. C. TOPPER and A. KLOOS (pers. comm.) respectively. As the *Cecropiaceæ s.s.* constitute a very homogeneous taxon and taking into account the fact that it has almost always been considered a natural group by taxonomists (with the exception of CHEW WEE-LEK, 1963, see intro-

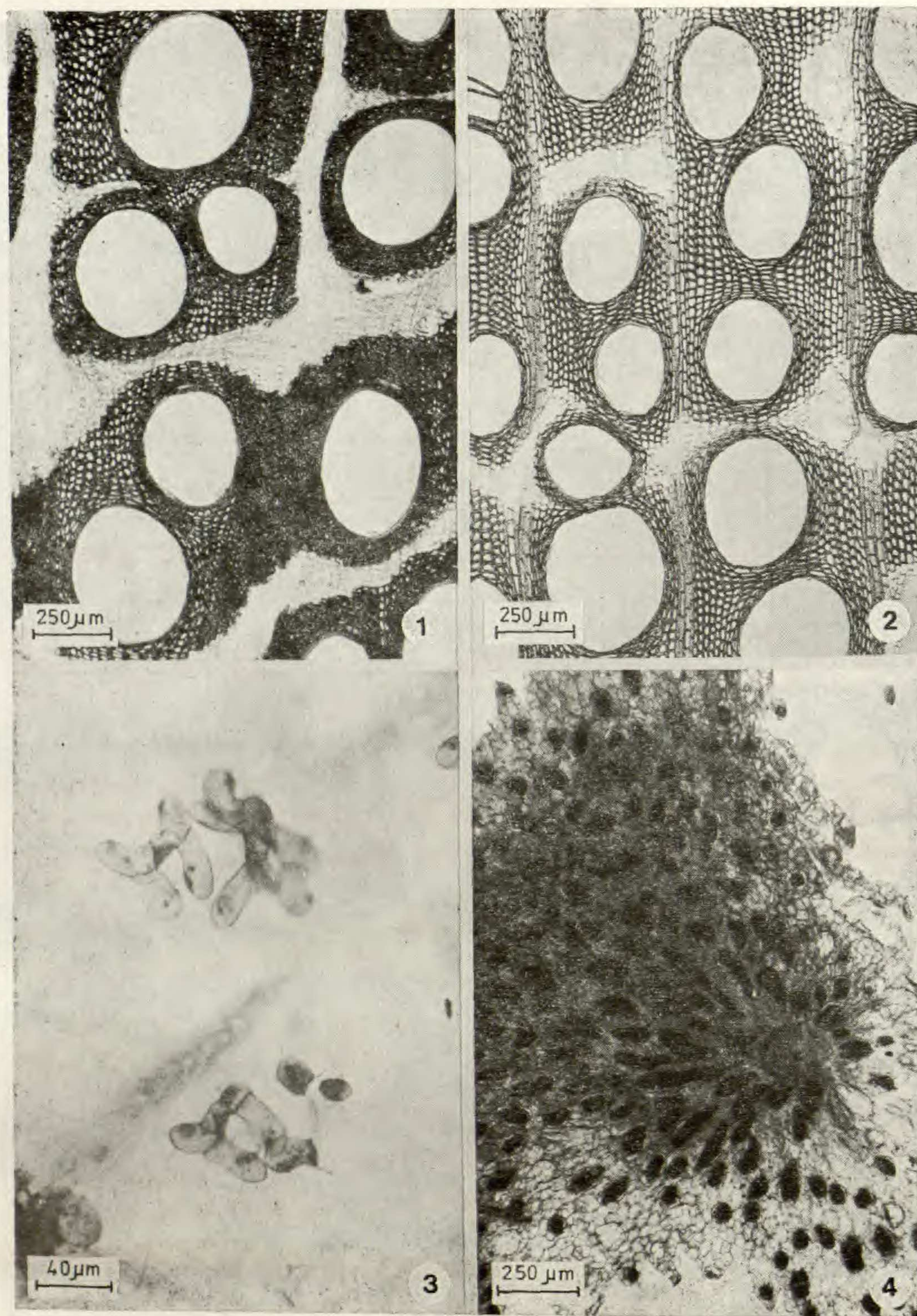
TABLE 6 : Some wood anatomical characters of the *Cecropiaceæ*.

|                            | Av. number of vessels per cluster | Av. number of vessels per sq. mm | Av. tang. pore diam. ( $\mu\text{m}$ ) | Av. vessel member length ( $\mu\text{m}$ ) | Av. fibre diam. ( $\mu\text{m}$ ) | Av. fibre length ( $\mu\text{m}$ ) | Av. multiseriate ray height ( $\mu\text{m}$ ) | Av. multiseriate ray width (cells) | Av. number of rays per mm | Paratr. par. distr. | Ray crystal type | Par. crystal type | Number of samples per species |
|----------------------------|-----------------------------------|----------------------------------|--|--|-----------------------------------|------------------------------------|---|------------------------------------|---------------------------|---------------------|------------------|-------------------|-------------------------------|
| <b>CECROPIA</b>            |                                   |                                  |  |  |                                   |                                    |   |                                    |                           |                     |                  |                   |                               |
| <i>C. burriada</i>         | 3(4)                              | 3                                | 175                                    | 630  | 28                                | 1 520                              | 1 050   | 4                                  | 7                         | v, a                | —                | —                 | 1                             |
| <i>C. concolor</i>         | 2(4)                              | 3                                | 155                                    | 505  | 50                                | 1 100                              | 890   | 3                                  | 7                         | v                   | —                | —                 | 1                             |
| <i>C. garcia</i>           | 3(5)                              | 2                                | 245                                    | —  | 35                                | —                                  | 1 530   | 3                                  | 4                         | v, a                | —                | rh                | 1                             |
| <i>C. obtusa</i>           | 3(5)                              | 3                                | 170                                    | 500  | 45                                | 2 000                              | 1 370   | 4                                  | 5                         | v, a                | rh               | —                 | 1                             |
| <i>C. peltata</i>          | 3(5)                              | 2                                | 200                                    | 565  | 30                                | 1 440                              | 1 010   | 3                                  | 5                         | v, a                | rh               | rh                | 1                             |
| <i>C. riparia</i>          | 2(5)                              | 1                                | 185                                    | 570  | 45                                | 1 660                              | 2 100   | 3                                  | 5                         | v, a                | —                | rh                | 1                             |
| <i>C. sciadophylla</i>     | 3(5)                              | 2                                | 260                                    | 620  | 30                                | 1 780                              | 1 380   | 4                                  | 4                         | v, a, c             | rh               | rh                | 10                            |
| <i>C. telealba</i>         | 3(4)                              | 2                                | 255                                    | 515  | 33                                | 1 500                              | 1 600   | 4                                  | 4                         | v, a                | —                | rh                | 1                             |
| <b>COUSSAPOA</b>           |                                   |                                  |  |  |                                   |                                    |   |                                    |                           |                     |                  |                   |                               |
| <i>C. angustifolia</i>     | 2                                 | 3                                | 295                                    | 565  | 25                                | 1 800                              | 960   | 3                                  | 4                         | a, c                | —                | rh                | 1                             |
| <i>C. asperifolia</i>      | 2                                 | 2                                | 290                                    | 595  | 25                                | 1 480                              | 1 050   | 5                                  | 6                         | c, b                | —                | rh                | 2                             |
| <i>C. batorum</i>          | 2                                 | 2                                | 275                                    | 520  | 25                                | 1 675                              | 1 100   | 4                                  | 7                         | c, b                | —                | rh                | 1                             |
| <i>C. contorta</i>         | 2                                 | 5                                | 220                                    | 320  | 20                                | 1 100                              | 665   | 4                                  | 5                         | c, b                | —                | rh                | 1                             |
| <i>C. latifolia</i>        | 2                                 | 2                                | 300                                    | 475  | 20                                | 1 760                              | 1 080   | 5                                  | 6                         | c, b                | —                | rh                | 1                             |
| <i>C. trinervia</i>        | 2                                 | 1                                | 250                                    | 550  | 20                                | 1 370                              | 1 080   | 4                                  | 7                         | b                   | —                | rh                | 1                             |
| <i>C. villosa</i>          | 2                                 | 2                                | 220                                    | 530  | 20                                | 1 600                              | 770   | 5                                  | 6                         | b                   | —                | rh                | 1                             |
| <b>MUSANGA</b>             |                                   |                                  |  |  |                                   |                                    |   |                                    |                           |                     |                  |                   |                               |
| <i>M. cecropioides</i>     | 2(4)                              | 1                                | 265                                    | 550  | 45                                | 1 500                              | 1 000   | 3                                  | 4                         | v                   | rh               | rh                | 9                             |
| <i>M. leo-errerae</i>      | 2(3)                              | 2                                | 210                                    | 460  | 35                                | 1 170                              | 920   | 4                                  | 3                         | v                   | rh               | rh                | 1                             |
| <b>MYRIANTHUS</b>          |                                   |                                  |  |  |                                   |                                    |   |                                    |                           |                     |                  |                   |                               |
| <i>M. arboreus</i>         | 3                                 | 3                                | 225                                    | 500  | 25                                | 1 550                              | 1 350   | 7                                  | 6                         | b                   | rh               | rh                | 5                             |
| <i>M. holstii</i>          | 3(5)                              | 5                                | 150                                    | 420  | 25                                | 1 400                              | 1 100   | 6                                  | 6                         | b                   | —                | rh                | 3                             |
| <i>M. libericus</i>        | 3(5)                              | 3                                | 200                                    | 500  | 25                                | 1 700                              | 1 360   | 7                                  | 5                         | b                   | rh               | rh                | 4                             |
| <i>M. serratus</i>         | 3(5)                              | 4                                | 140                                    | 450  | 25                                | 1 110                              | 1 050   | 5                                  | 5                         | b                   | —                | rh                | 1                             |
| <b>POIKILOSPERMUM</b>      |                                   |                                  |  |  |                                   |                                    |   |                                    |                           |                     |                  |                   |                               |
| <i>P. naucleiflorum</i>    | 2                                 | 5                                | 260                                    | 325  | 25                                | 660                                | comp.   | 5                                  | 2                         | v, unign.           | —                | rh, dr            | 1                             |
| <i>P. suaveolens</i>       | 2                                 | 9                                | 310                                    | 350  | 25                                | 865                                | comp.   | 6                                  | 2                         | v, unign.           | —                | rh, dr            | 2                             |
| <b>POUROUMA</b>            |                                   |                                  |  |  |                                   |                                    |   |                                    |                           |                     |                  |                   |                               |
| <i>P. acuminata</i>        | 3(4)                              | 5                                | 170                                    | 615  | 25                                | 1 310                              | 990   | 4                                  | 6                         | a, c                | —                | rh                | 1                             |
| <i>P. acutiflora</i>       | 2(4)                              | 3                                | 195                                    | 530  | 25                                | 1 445                              | 820   | 3                                  | 8                         | a, c                | rh               | rh                | 1                             |
| <i>P. apiculata</i>        | 2(3)                              | 3                                | 250                                    | 600  | 25                                | 1 510                              | 875   | 4                                  | 4                         | v, a                | —                | —                 | 1                             |
| <i>P. aspera</i>           | 2(4)                              | 3                                | 200                                    | 580  | 30                                | 1 220                              | 650   | 3                                  | 5                         | a, c                | rh               | rh                | 1                             |
| <i>P. cecropiifolia</i>    | 2                                 | 3                                | 180                                    | 650  | 25                                | 1 600                              | 900   | 3                                  | 7                         | a, c                | rh               | rh                | 2                             |
| <i>P. chocoana</i>         | 2                                 | 6                                | 175                                    | 475  | 20                                | 940                                | 745   | 3                                  | 6                         | a, c                | —                | rh                | 1                             |
| <i>P. digitata</i>         | 2(3)                              | 2                                | 190                                    | 500  | 25                                | 1 280                              | 950   | 3                                  | 6                         | a, c                | rh               | rh                | 2                             |
| <i>P. guianensis</i>       | 2-3                               | 4                                | 200                                    | 680  | 30                                | 1 300                              | 850   | 3                                  | 5                         | a, c                | —                | rh                | 4                             |
| <i>P. hirsutipetrolata</i> | 2(4)                              | 2                                | 220                                    | 845  | 30                                | 1 690                              | 905   | 3                                  | 5                         | v, a                | rh               | rh                | 1                             |
| <i>P. laevis</i>           | 2(3)                              | 2                                | 240                                    | 580  | 35                                | 1 475                              | 1 020   | 3                                  | 7                         | v                   | —                | rh                | 1                             |
| <i>P. maroniensis</i>      | 2(3)                              | 2                                | 210                                    | 550  | 30                                | 1 500                              | 1 000   | 4                                  | 6                         | v, a                | —                | rh                | 2                             |
| <i>P. melinonii</i>        | 2(4)                              | 3                                | 210                                    | 620  | 30                                | 1 600                              | 700   | 3                                  | 5                         | v, a                | —                | rh                | 2                             |
| <i>P. mollis</i>           | 2(4)                              | 2                                | 225                                    | 610  | 30                                | 1 550                              | 990   | 3                                  | 5                         | v, a                | —                | —                 | 1                             |
| <i>P. ovata</i>            | 2(3)                              | 3                                | 225                                    | 550  | 25                                | 1 300                              | 785   | 4                                  | 8                         | b                   | —                | rh                | 1                             |
| <i>P. substrigosa</i>      | 2                                 | 3                                | 215                                    | 600  | 25                                | 1 420                              | 720   | 4                                  | 5                         | a, c                | rh               | rh                | 1                             |
| <i>P. triloba</i>          | 2(3)                              | 2                                | 255                                    | 590  | 25                                | 1 600                              | 2 280   | 5                                  | 4                         | a, c                | rh               | rh                | 1                             |

Legend : v = vasicentric ; a = aliform ; c = confluent ; b = banded ; unign. = unignified apotracheal parenchyma ; rh = rhombic crystals ; dr = druses ; comp. = vertically compounded.

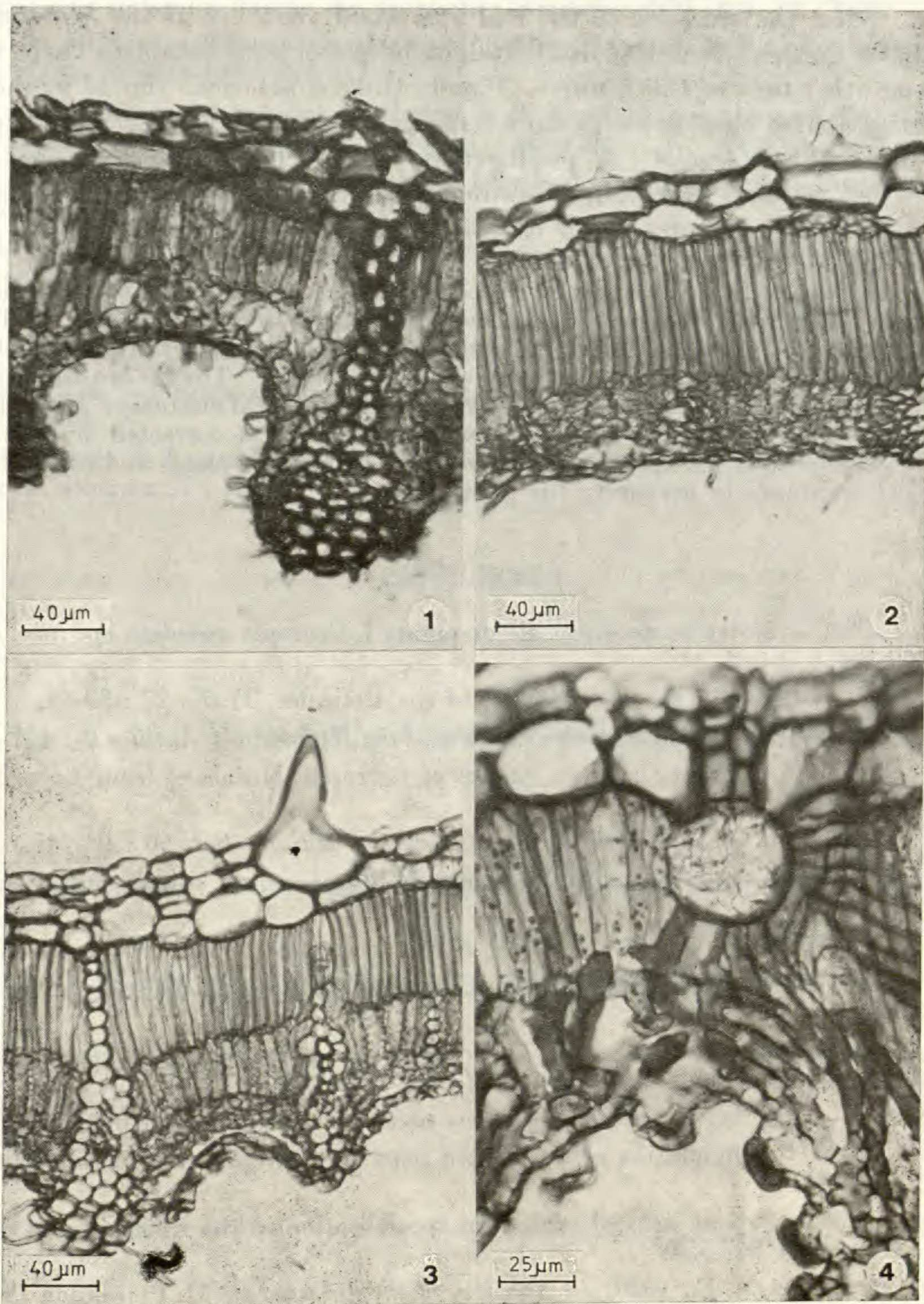


Pl. 2. — *Cecropia sciadophylla* Mart. (Maguire & al. 55577) : 1, T. S. of the wood. — *Musanga cecropioides* R. Br. (ex MAD-SJR $\omega$  15799) : 2, T. S. of the wood. — *Coussapoa latifolia* Aubl. (Lindeman & Heyde 78) : 3, T. S. of the wood. — *Myrianthus libericus* Rendle (ex MAD $\omega$  36781) : 4, T. S. of the wood.



Pl. 3. — *Poikilospermum naucleiflorum* Euse (*RTIw 1507/i22-H 1868-274*) : 1, T. S. of the wood. — *Urera hypselodendron* (Horhst.) Wedd. (*Schlieben 1721*) : 2, T. S. of the wood. — *Poikilospermum subtrinervium* (Miq.) Chew (*Mandi 25*) : 3, glands on adaxial leaf surface. — *Poikilospermum amboinense* Zipp. ex Miq. (*van Leeuwen s.n.*) : 4, Cystoliths around a hydathode on adaxial leaf surface.





Pl. 4. — *Myrianthus arboreus* Pal. Beauv. (*Deistel* 428) : 1, T. S. of the lamina showing bundle sheath extension, prominent vein and papillated abaxial epidermal cells. — *Cecropia surinamensis* Miq. (*L.B.B.* 12739) : 2, T. S. of the lamina showing epidermal cells with silicified outer walls. — *Cecropia latiloba* Miq. (*Prance & Berg P* 17586) : 3, T. S. of the lamina showing conical papilla, intermediate layer and some arachnoid hairs. — *Pourouma laevis* Benth. (*Boschwezen* 4010) : 4, T. S. of the lamina showing a large druse.

duction), it seems justified to place this taxon in the *Moraceæ* based on the characters studied here. After the students of the leaf and wood anatomy of the *Moraceæ*, mentioned before, have finished their research it might be possible to establish their taxonomic position among other taxa of this family. Finally these conclusions should be incorporated in a re-investigation of the (flower) characteristics used by BERG (1978) to separate the *Cecropiaceæ* from the *Moraceæ*. A phylogenetic approach of this taxon has not been carried out. This requires a profound anatomical investigation of all related taxa, which will be done by TOPPER (in prep.) and KLOOS (in prep.).

ACKNOWLEDGEMENTS : C. C. BERG and E. G. B. KIEFT are gratefully acknowledged for the fast identification of various herbarium vouchers. The discussions with S. M. C. TOPPER and A. KLOOS concerning the data sets of our and their material, and more in general the value of wood and leaf anatomical characters in taxonomy were very helpful. Thanks are due to Dr. P. BAAS and A. M. W. MENNEGA for their advises especially concerning the leaf anatomy. Prof. Dr. E. HENNIPMAN critically read the manuscript. The english version was corrected by Miss L. COBB. Finally we are grateful to H. RYPKEMA for preparing the figures and plates and to H. ELSEENDOORN for his technical assistance in preparing the photographs.

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